AN EXPLANATION FOR THE DISCREPANCY IN THE CHROMOSOME COUNT OF THE REDBUD (*CERCIS CANADENSIS*, LEGUMINOSAE)

WILL H. BLACKWELL

Department of Botany, Miami University
Oxford, OH 45056, U.S.A.

ABSTRACT

Varying chromosome counts of *Cercis canadensis* L. have been reported in the literature, i.e., $n = 6$ and $n = 7$. Squash preparations of pollen parent cells from native trees in southwestern Ohio confirm the count of $n = 7$. However, past segmental interchanges between nonhomologues are the assumed cause of occasional structural connections observed between two or more bivalents during meiosis. The viewing of such connected chromosomes, perhaps superficially appearing as a unit structure, might result in an erroneous count, such as $n = 6$.

A plant species with a low number of chromosomes usually does not present special difficulty in the determination of chromosome number unless aneuploidy or dysploidy exists in its populations (cf. *Claytonia virginica*, Lewis 1967). *Cercis canadensis*, a woody legume, is not known to be aneuploid or dysploid, yet different base chromosome numbers have been reported. Senn (1938) reported $n = 6$ and $2n = 12$, based on both meiotic and mitotic counts at the Blandy Experimental Farm, Virginia. These counts had impact in the framework of Senn's pioneering work on legume cytology in relation to phylogeny. However, Taylor (1967) reported $n = 7$ for *Cercis canadensis* from a "shrub of unknown origin in Dominion Arboretum. Ottawa." Curtis (1976) subsequently reported $n = 7$ from a specimen cultivated at the Missouri Botanical Garden, and suggested that the $n = 6$ determination (by Senn) was incorrect. But would a diligent worker such as Senn have made an actual miscount on a species as seemingly simple chromosomally as the redbud? The argument takes on additional significance in light of Goldblatt's (1981) view of *Cercis* as a diploid ($2n = 14$, $n = 7$, $x = 7$) relict in the subfamily Caesalpinioideae, most members of which are presumably tetraploids — often $n = 14$, but some $n = 12$! In *Cercis*, the ancestral diploid condition is considered to be retained, not only in context of the caesalpinioids, but in that of the legumes as a whole. However, does variation in the chromosome number of *Cercis* occur? Is it uniformly $n = 7$ as one would suspect, or do counts of $n = 6$ exist as well?

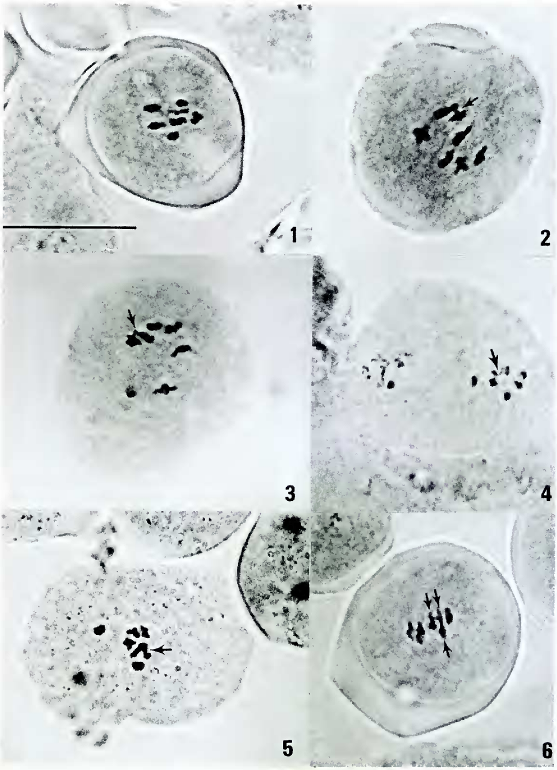
Over the course of three successive springs (centering around early

SIDA 14(1):7 – 11. 1990.

April), I obtained meiotic pollen parent cell (PPC) counts from four trees at different locations among the native populations of redbud in southwestern Ohio (Butler County). These specimens are vouchered in the Herbarium of Miami University (MU). Standard aceto-carmine smear methods were employed in all cases. Prior to staining, flower buds were fixed in modified Carnoy's solution (4 parts chloroform, 3 parts absolute ethanol, and 1 part glacial acetic acid). Buds containing appropriate meiotic stages were collected typically between 7:00 and 7:30 A.M.

I was surprised by finding apparent counts of $n = 7$, $n = 6$, and even lower numbers, in all trees (Figs. 1 – 6). However, careful anaylsis by oil-immersion light microscopy, photography, and enlargement of photographic prints revealed that the actual count is $n = 7$ (Fig. 1). This count ($n = 7$) could be documented in the case of each tree. In the squashes, however, associations were rather commonly observed between two or more of the bivalents during at least the first prophase/metaphase of meiosis I. These associations may occur to an extent that chiasma-like structural connections exist for a time between nonhomologues (Figs. 2 – 3). These connections may persist, as observed between nonhomologous univalents in telophase of meiosis I (Fig. 4). The fact that some cells in a given smear show only unassociated bivalents, while others show apparently catenated chromosomes, is not altogether surprising because plants with reciprocal translocations can occasionally produce a "normal" complement of bivalents at meiosis (reported, but as rare, in *Collinsia heterophylla* by Garber and Dhillon 1962). Regardless, the associations in *Cercis canadensis* provide some evidence of a past (perhaps long past) segmental interchange (Burnham 1956) between two or more of the chromosome pairs.

Associations between nonhomologous chromosomes are known within another member of the legume family (lines of garden pea, *Pisum sativum*, $n = 7$, cf. Sansome 1932). Although similar to those of the garden pea, the associations in redbud are not as consistently present, nor necessarily as definitive. The chromosomal connections in *Cercis* are nonetheless in some cases striking enough to result in the appearance of a chain of four (or more) chromosomes at diakinesis (Fig. 5). This chain in redbud bears a close resemblance to the often-cited, excellent photographic illustration of a translocation chain or ring of four chromosomes described by Brown (1949) in irradiated tomatoes. That the associated chromosomes in *Cercis* are merely connected at a point (Figs. 2 – 3) and appear at most connected as a chain (Fig. 5) and not as an actual ring is probably indicative of the past interchange of only small chromosomal segments (Burnam 1932). Nonetheless, to a cytotaxonomic investigator who had not studied the situation in *Cercis*, a count other than the correct one of $n = 7$ might be made,



FIGS. 1 – 6, PPC's of *Cercis canadensis*: Fig. 1, late prophase of meiosis division I, $n = 7$. Figs. 2 – 3, late prophase of meiosis I; note connections between two bivalents (arrows). Fig. 4, telophase of meiosis I; note persistence of connection between two univalents (arrow). Fig. 5, late prophase of meiosis I; note apparent count of six due to chromosome chain involving two bivalents (arrow). Fig. 6, metaphase of meiosis I; count of four or five is possible due to interconnection of bivalents (arrows). Scale bar, 20 μm; all photographs are at same magnification.

especially if a cell such as that in Figure 5 would be encountered. Even if bivalents are merely "interlocked" (a condition reported as common in diploid species of *Tradescantia*; Sax and Anderson 1933), an opportunity for a miscount would exist. It seems plausible that Senn (1938) encountered either very closely associated, perhaps interlocked, bivalents, or else an actual reciprocal translocation, when he reported his count of $n = 6$ from PPC's. Close spatial association of nonhomologues may give rise to natural reciprocal translocations, (suggested as a possiblility by Sax and Anderson 1933). Such translocations may be observed in somatic tissue as well as cells undergoing meiosis (Burnham 1956). Hence, Senn's $2n$ (somatic) count of 12, made from anther wall tissue, is also understandable in the light of the interpretation(s) presented here. Regardless, the chromosome count of all species of *Cercis*, although perhaps difficult to determine in the case of *C. canadensis*, is apparently $n = 7$, $2n = 14$, as considered by Goldblatt (1981).

Study of the cytology of species of *Cercis* other than *C. canadensis* might prove interesting if only to determine if nonhomologous chromosome associations exist in these as well. Since chromosomal connections due to reciprocal translocations may result in varying levels of reduced fertility (Garber 1948), a study of pollen viability (or an analysis of microspore quartets) might be undertaken as well.

ACKNOWLEDGMENTS

I acknowledge the help of Julie A. Ballenger and Michael A. Vincent for assistance with collection of some of the bud and voucher material utilized in this study. I am appreciative of the helpful suggestions of Drs. Roy C. Brown, Thomas G. Lammers, and Áskell Löve during the preparation of this manuscript.

REFERENCES

BROWN, S.W. 1949. The structure and meiotic behavior of the differentiated chromosomes of tomato. Genetics 34:437 – 461.

BURNHAM, C.R. 1932. An interchange in maize giving low sterility and chain configurations. Proc. Natl. Acad. Sci. 18:434 – 440.

______. 1956. Chromosomal interchanges in plants. Bot. Rev. 22:419 – 552.

CURTIS, W.F. 1976. Chromosome counts in *Grielum* and *Cercis*. Ann. Missouri Bot. Gard. 63:379 – 380.

GARBER, E.D. 1948. A reciprocal translocation in *Sorghum versicolor* Anderss. Amer. J. Bot. 35:295 – 297.

______ & T.S. DHILLON. 1962. The genus *Collinsia*. XVII. A cytogenetic study of radiation-induced reciprocal translocations in *C. heterophylla*. Genetics 47:461 – 467.

GOLDBLATT, P. 1981. Cytology and the phylogeny of Leguminosae. Pp. 427 – 463 in,

R. M. Polhill & P. H. Raven eds. Advances in Legume Systematics. Part 2. Royal Botanic Gardens, Kew.

LEWIS, W.H., R. L. OLIVER, & Y. SUDA. 1967. Cytogeography of *Claytonia virginica* and its allies. Ann. Missouri Bot. Gard. 54:153 – 171.

SANSOME, E.R. 1932. Segmental interchange in *Pisum sativum*. Cytologia 3:200 – 219.

SAX, K. & E. ANDERSON. 1933. Segmental interchange in chromosomes of *Tradescantia*. Genetics 18:53 – 67.

SENN, H.A. 1938. Chromosome number relationships in the Leguminosae. Bibliogr. Genet. 12:175 – 336.

TAYLOR, R.L. 1967. In IOPB chromosome number reports XIII. Taxon 16:456.